Double Hydrocœle in the Development and Metamorphosis of the Larva of Asterias rubens, L.

By

James F. Gemmill, M.A., D.Sc.

With Plates 6 and 7.

CONTENTS.

As is well known, the hydrocœle or water vascular system of Echinoderms arises from a portion of the left cœlom. The early larvæ being bilaterally symmetrical, a great deal of discussion has taken place as to whether any definite portion of the right cœlomic cavity corresponds with the hydrocœle, and if so, whether this portion gives rise to any adult structure which can be identified. There has also been much speculation regarding the bilateral ancestor. On both of these problems a study of double hydrocœle—that is, the condition in which a right as well as a left hydrocœle appears—is calculated to throw light. While this is true for any kind of Echinoderm, it applies particularly in the case of A. rubens, since there is evidence that the ontogenetic history of our species belongs to the least modified type of larval development we yet know of within the phylum (**4**, p. 279). Again, various points in normal development are difficult to determine with certainty, on account of the great and rapid change of symmetry which occurs at metamorphosis. Welcome additional light on a number of these points (p. 72) has accrued from a study of double hydrocœle.

Normal Development up till Metamorphosis.

(c f. Pl. 6, fig. 1).

It is advisable at this stage to give a brief account of the formation of the hydrocœle in normal larvæ, and also of the subsequent course of development till the commencement of metamorphosis, mentioning only those points which are of importance in connection with double hydrocœle. The complete account appears elsewhere (**4**).

The two enterocœles arise separately, one from each side of the anterior end of the archenteron, and, as a rule, the left one alone acquires a hydroporic opening. During the early growth of the larva the enterocœles extend forwards into the preoral lobe, and backwards over the lateral aspects of the stomach. At about the twenty-first day the enterocœles unite across the middle line in the preoral lobe. The front portion of each enterocœle may now be called the anterior cœlomic region[1] (*l. a. c.* or *r. a. c.*). Shortly thereafter each enterocœle begins to show a constriction just behind the level of the hydropore. By gradual extension of these constrictions, from the dorsal to the ventral side, the right and left posterior cœloms (*r. p. c.* and *l. p. c.*) are cut off from the corresponding middle cœlomic regions[1] (*r. m. c.* and *l. m. c.*). Before this process is complete the left posterior cœlom has begun to grow more rapidly than the right one, and in particular has sent out a ventral and a dorsal horn. The former pushes its way to the right, across the middle line between stomach and rectum, and its extremity undergoes expansion, and finally comes to lie against the ventral corner of the right middle cœlomic region. Shortly afterwards the intervening septum breaks down, so that now the right middle and the left posterior cœlomic regions are in communication with one another. The right middle cœlomic region ceases to undergo further differentiation or to increase markedly in size. On the other hand, the left middle cœlomic region,

[1] The terms anterior and middle cœloms or cœlomic regions are used here for descriptive convenience and not as indicating separate structural or morphological units (see **4**, p. 254).

into which the hydropore opens, being at this stage completely isolated from the two posterior cœloms, begins to undergo expansion and to exhibit the five hydrocœle pouches which are the rudiments of the rays of the water vascular system. Still later, the dorsal horn of the *l. p. c.* acquires a secondary opening into the left middle cœlomic region on the deep aspect of the interval between pouches I and II.[1] Meantime the ventral horn of the *l. p. c.* has extended so as to enclose the rectum (cf. 4, Pl. 18, fig. 7), while the rudiment of the calcareous plate for ray I has appeared superficial to the cavity derived from the expanded extremity of this horn, to the right of the midventral line. The other four arm-rudiments with their terminal ossicles, all overlying the margin of the *l. p. c.*, have also appeared, the series beginning with arm-rudiment II, behind and to the left of the hydropore. Between arm-rudiments II and I is the aboral brachiolarian notch, the last-named rudiment being formed on the opposite side of the notch from hydrocœle pouch I, although the rudiment in question afterwards becomes associated with hydrocœle pouch I to form ray I of the adult starfish. Interradial ossicle I–II develops over the dorsal sac, but the other interradials and the dorso-central are superficial to the (larval) right posterior, or epigastric, cœlom.

The dorsal sac or madreporic vesicle develops from mesenchymal cells at or near the mid-dorsal line, becoming evident as a vesicle about the twenty-fifth day, and showing rhythmic contractility eight or ten days later. It is the floor of the sac which pulsates, and the effect is to displace the fluid in the underlying spongy tissue, the tissue becoming turgid and bulging up the floor of the sac in the intervals between the contractions. Owing to the absence of vessels we cannot say that there is a definite circulation in the larva, while the adult hæmal system is still a subject of discussion. However, there is reason for thinking that the dorsal sac and underlying spongy tissue serve as a heart-complex (4, p. 219), and that the general result even in the larva is to distribute nutritive fluid absorbed from the stomach (see further on, p. 58).

Double Hydrocœle up till Metamorphosis.

(Pl. 6, figs. 1–5, and Pl. 7, figs. 10–12.)

It is impossible to tell what larvæ will develop double hydrocœle until a little after the time when the opening of the

[1] The numbering of the rays adopted in this paper is as follows: On the aboral side passing sinistrally (i.e. counter-clockwise) from the madreporite we come in series to rays II, III, IV, etc., while ray I is immediately dextral to the madreporite (see 4, p. 276).

ventral horn of the *l. p. c.* into the right middle cœlomic region ought to be effected, and the earliest sign of double hydrocœle I could recognise was that in certain cases, without there being any permanent failure of health, the ventral horn of the *l. p. c.* did not succeed in forming the communication in question. Two different environmental factors may be concerned in evoking this condition (see p. 70). The first, less common and of less importance, is a disturbance of growth due to temporary malnutrition, in virtue of which the ventral horn of the *l. p. c.* does not exhibit sufficient preponderance to carry it over to the right side of the rectum. Accordingly, the horn in question has not the opportunity of meeting and uniting with the ventral corner of the right middle cœlomic region, which thus remains isolated from the cœloms behind it, exactly like the left middle cœlomic region. However, sooner or later, if there is further growth, the ventral horn of the *l. p. c.* meets and unites with the ventral angle (ventral horn) of the *r. p. c.*, which has meantime advanced towards it, and from the common cavity thus formed a hollow sheath begins to extend around the rectum. We have now an absence of that polarity between the right and left sides which should be present at this critical stage in the development of the larva. Two courses are open: (*a*) There may be failure of further differentiation, including failure of formation, or a rudimentary condition, of the hydrocœle pouches even on the left side; (*b*) the right and left middle and posterior cœlomic regions may proceed to differentiate more or less symmetrically, the left side imposing its course of development on the right one and causing, through secondary homœosis (p. 71), the formation of a right as well as of a left hydrocœle.

The second, and much the more important of the environmental factors concerned in evoking double hydrocœle, appears to be excessive nutrition. The larvæ in one or two of my cultures grew very rapidly, their stomachs becoming widely expanded and globular. The ventral horn of the *l. p. c.* thus had too great a distance to travel before it could unite with the right middle cœlomic region, and accordingly the union in question did not take place, the last-named cavity being left isolated from the posterior cœloms, as in the different mode of causation already described. The effect, however, is the same if differentiation proceeds. The left cavities impose their developmental symmetry on the right ones, one of the results being the formation of double hydrocœle.

In all such cases the chief points in aberrant development which have to be noted prior to metamorphosis, have reference to the following structures : hydrocœle pouches, stone canal grooves, posterior and pharyngeal cœloms, the aboral arm-rudiments, and the skeletal ossicles. The preoral structures develop along normal lines.

The **hydrocœle pouches** appear on the right side either at the same time as on the left, or very slightly later. The sequence in their formation is the same on both sides, that is to say, III and IV are the first to become evident, then II and V, and I very slightly later. Towards the end of larval life, a secondary opening forms between the dorsal horn of the *r.p.c.* and the *r.m.c.* exactly like that between the dorsal horn of the *l.p.c.* and the *l. m. c.* The **stone canal groove** appears on the right side as definitely as on the left, and in a corresponding position. There does not, however, appear to be any tendency to the formation of a right pore canal.

It was noted above (p. 52) that the right and left **posterior cœloms** unite with one another around the rectum through fusion of their ventral horns. A communication,[1] which has no homologue in the normal development of A. rubens, is next established between the two cœloms dorsally, owing to the formation of a larger or smaller perforation in the

[1] The formation of this opening in double hydrocœle is no doubt traceable to the normal tendency of the dorsal horn of the *l. p. c.* to meet and unite with the ventral horn of the same cavity during metamorphosis in order to complete the circle of the hypogastric cœlom. Curiously enough Delage (see **4**, p. 244) describes the presence of a dorsal opening between the *l. p. c.* and the *r. p. c.* as being normal for the late larva of A. glacialis.

dorsal mesentery. Elsewhere, the posterior cœloms are separated by the mesentery in question, the layers of which in some instances are closely apposed and in others are separated by a wide intervening space. The last-named difference depends on whether the disc-rudiments are broad or not, and this, in turn, depends chiefly on the size of the stomach. The space between the mesenteries, when well-marked, takes on a sparsely cellular character, the cells being round rather than branched, and the space itself becoming pseudo-cœlomic. A true lining membrane is of course absent, but interradial ossicles may develop over the space as they do normally over the right larval (epigastric) cœlom. It was noted earlier, in connection with the middle cœloms, that an opening appears between each and the corresponding posterior cœlom, exactly like the opening normally present in late larvæ between the *l. m. c.* and the dorsal horn of the *l. p. c.*

The **pharyngeal cœlom** develops on the right side as well as on the left, in the form of an evagination from the dorsal horn of the posterior cœlom, which passes first inwards towards the middle line; then curves ventralwards and finally forwards within the root of the mesentry separating the posterior cœlom from the hydrocœle. At first the two pharyngeal cœloms are separate from one another, but in late larvæ and in specimens which are undergoing or have undergone metamorphosis they are found to be united across the middle line for a short portion of their length not far from their places of origin. This mesial portion may extend backwards for some distance on its own account, so as to appear an independent cavity in transverse sections which show the two pharyngeal cœloms separated laterally from one another (cf. Pl. 7, figs. 13, 16).

Aboral **arm-rudiments** I are not developed, while arm-rudiments II to V meet back to back, forming a paired series of (right and left) elements, which together give rise to a strap-like "disc" overlying the dorsally convex aspect of the larval body (cf. Pl. 6, figs. 4, 5). A **terminal ossicle** appears in each of the arm-rudiments. Of the **interradial ossicles,** that which overlies the dorsal sac, viz. interradial I–II, is practically always present and is always, so far as I have observed, a single piece. Interradial V–I is never found. The other interradials, viz.: II–III, III–IV and IV–V are absent as a rule, but if the stomach is unusually large and the "disc" broad, they may be present in pairs (see Pl. 6, fig. 4). When present they develop not over an epigastric cœlom, but over a pseudo-cœlomic space between the layers of the dorsal mesentery (pp. 56, 64). It may be of importance as regards the homologies of the skeleton in different echinoderms to recognise that the asterid interradial I–II is different from the other interradials, in respect that it arises over the dorsal sac and is therefore essentially unpaired and mesial in position, as we find it in double hydrocœle. When the spines appear, so far as space allows, they develop just in the same number and position as in normal larvæ. Thus in a specimen with broad "disc," at the commencement of metamorphosis, twelve spines may be counted over each of the terminal plates (cf. **4**, p. 266).

It remains to be added that during all this time, the anterior and middle portions of the larva have been developing along perfectly normal lines. Even the same kinds of variation as are found in ordinary larvæ (**4**, p. 236), occur also in double hydrocœle, for example, the presence of three or more papillæ on each side of the sucker instead of only two, entire absence of the median dorsal process, variation in the length of ciliated processes, and in particular great shortening of the postero-lateral process on the right side.

Normal Metamorphosis.

We must preface the description of metamorphosis in double hydrocœle with a short account of normal metamorphosis. At the commencement the brachia give temporary attachment, but definitive fixation takes place by means of the sucker. the cells of which secrete a strongly adhesive cement. The whole anterior part of the larva including the ciliated processes becomes retracted and is finally amalgamated with the oral (left larval) aspect of the disc, considerable histolysis, both of epidermal and mesenchymal tissues taking place during the process. A stalk, which soon becomes solid, is left connecting the sucker with the oral aspect of disc. In the end this stalk, which has meantime grown slender and elongated, ruptures near the disc, sucker and stalk being left behind. The stalk-cavity before its disappearance, is seen to be encircled by the just completed hydrocœle ring, as in Asterina (MacBride **6**, p. 356), and Solaster (Gemmill **3**, p. 27). The larval mouth closes and the larval œsophagus becomes divided near the junction of its stomodæal and endodermal portions, the former joining the epiderm of the (starfish) oral surface, and the latter being taken into the stomach wall through gradual widening of the cardiac orifice. The anus and terminal part of the rectum in the larva degenerate, but the larval intestine and the rest of the rectum are retained to form the intestine and rectal sac of the adult. The paired radial cæca grow out from the aboral (pyloric sac) region of the stomach. The permanent mouth and anus are new formations, the latter appearing aborally in interradius I–V.

The right middle cœlomic (right hydrocœlic) region is early obliterated. The common mesial portion of the right and left anterior cœlomic regions at first become greatly expanded by taking the rest of these cavities into itself. For a time it reaches some distance into the stalk, but it becomes gradually smaller, and finally disappears. Hydrocœle, internal oral circular sinus (inner perihæmal ring), axial sinus, stone canal, and axial organ are products of the left middle cœlomic region. The larval *r. p.c.* and *l. p. c.* become respectively the epigastric and hypogastric cœloms. The pharyngeal cœlom forms a ring round the mouth on the oral aspect of the stomach, and is afterwards practically amalgamated with the hypogastric cœlom through formation of interradial and radial perforations in the intervening mesentery, whereby the adradially placed oral gastric ligaments are left.

The dorsal sac of the larva persists as the dorsal sac of the adult, the reticular tissue underneath it being invaginated upwards and forming the so-called head process or glandular process of the axial organ. The axial organ appears as a fold-like thickening of the walls of the *l. m. c.*, running parallel with the stone canal. It consists at first of spongy hæmal tissue, in which, however, cells of parenchymatous nature soon appear. The origin of these cells is ascribed by MacBride to downward growth from the gonad rudiment (**6**), but I think they are derived simply from the lining of the *l. m. c.* (**4**, p. 261).

It is probable that nutriment (absorbed from the stomach, the pyloric sac, and the pyloric cæca) passes by way of the gastric hæmal tufts to the axial organ, and then (*a*) through the hæmal tissue within the aboral perihæmal sinus to the genital organs; and (*b*) down the hæmal channels of the axial organ to the internal oral hæmal ring and the radial hæmal strands. supplying nourishment in particular to the central nervous system, the sucker feet, and the muscles of the ambulacral ossicles. The head process of the axial organ, being invaginated into the dorsal sac, acts as a heart. or, at any rate. as a pulsating spongy ampulla at the nodal point in this circulation. The severance of the nutritive and the respiratory functions in Echinoderms is probably the key to the peculiarities of the hæmal system in this phylum.

Metamorphosis in Double Hydrocœle.

(Pl. 6, fig. 6, and Pl. 7, fig. 9, surface views; Pl. 7, figs. 14–18, sections.)

We find the same signs of approaching metamorphosis here as in normal development. The brachia move actively in all directions and not infrequently effect temporary adhesion to smooth surfaces. At the same time, longitudinal contractions of the body-wall begin to take place, tending to dilate the median cavity in the preoral lobe, and to push out the sucker. A little later, attempts at sucker fixation occur, and in the end cement fixation takes place, not without several short periods of temporary attachment, which are effected in the manner I described for normal larvæ before the gland cells of the sucker shed their cement and thus produce final fixation (**4**, p. 250). In the intervals between the temporary attachments just referred to, the brachia are the adhering organs, and the starfish may be described as crawling by the combined action of brachia and sucker. The larva is now shrinking slightly in size, and as its tissues are becoming more condensed it is no longer able to swim freely up from the bottom by the help of its ciliated processes.

After fixation has taken place the longitudinal contractions of the body-wall become stronger and more regular, and under their influence the whole of the preoral lobe is gradually pulled towards the disc or body portion of the larva. Since in double hydrocœle the right and left sides of the larval body are symmetrical and the aboral arm rudiments, etc., so far as they are represented, overlie the dorsal aspect of the larval body, we find that as metamorphosis proceeds the preoral lobe structures, including the sucker and the larval mouth, are retracted towards the mid-ventral line, and, as no torsion of preoral lobe on body of larva takes place, the remains of the larval mouth comes to lie approximately in the middle of the ventral surface while the sucker is in the mid-ventral line anterior to this part. An extremely early stage at the very commencement of metamorphosis is shown in lateral view in Pl. 6, fig. 5, and a later stage with retraction well advanced in Pl. 6, fig. 6. During these changes the mesenchyme throughout the anterior portion of the larva and within the ciliated processes breaks down, and becoming semi-fluid is transferred into the disc in the same manner as in normal development. In the end the preoral structures are reduced till only the sucker and a long slender stalk are left, the latter projecting from the mid-ventral line in the position previously indicated. The last remains of stalk and sucker are not absorbed, but are left to disintegrate, rupture taking place at the junction of stalk and body. This very interesting fact, which I found to occur normally in the metamorphosis of A. rubens, was actually first observed by me in the case of a double hydrocœle specimen, namely, that represented in Pl. 7, fig. 8. In this figure we are looking at the left aspect of the bilateral "starfish," there being five rays on the right side, not seen in the drawing, but entirely similar to the five rays on the left side. There is no question as to which are the anterior and posterior ends of the strap-like "starfish," reckoning by the hydrocœle lobes. The first of the hydrocœle lobes has not an aboral arm-rudiment of its own, since, as we saw above, aboral arm-rudiment I is not developed in double hydrocœle larvæ. The dorsal sac or madreporic vesicle lies in the middle line close under the dorsal surface at the anterior end. When in due course this young "starfish" became separated from its stalk and crawled away it used its sucker feet like an ordinary starfish, resting apparently with indifference at one time chiefly on its right, and at another chiefly on its left sets of sucker feet. In shape it was more convex dorsally than would appear from Pl. 7, fig. 8, in which, for purposes of illustration, it is partly straightened out. A mouth was formed in the ordinary way, but the formation of an anus could not be made out. The "starfish" lived for five or six weeks after breaking away from its stalk, and seemed to be attracted by small portions of animal tissue (shredded ovary of sea urchin), which were placed in the vessel containing it. Unfortunately a satisfactory histological examination was rendered impossible owing to the fact that the specimen became unhealthy when I was away during part of the autumn vacation, and on my return had suffered such degeneration that, though still alive, it proved useless for the study of finer details when cut into serial sections. However, several other double hydrocœle specimens were obtained at various stages in metamorphosis, and an examination of serial sections of these specimens allowed the following facts to be made out.

The Stalk.—Since the adjacent ends of the two (half) rings of the hydrocœle do not actually unite (p. 63), we cannot speak of the stalk being encircled by the ring canals of the hydrocœle, although insertion of stalk into disc falls well within the area virtually enclosed by these canals. It would be a point of no little interest to determine whether the base of the stalk is surrounded by the circular oral nerve area. In the specimen previously referred to this seemed to be the case as far as one could judge by external observation, while examination of sections of another specimen at a relatively early stage in metamorphosis led, though not quite decisively, to the same conclusion. In normal development the base of the stalk is not surrounded by the circular oral nerve. Probably in double hydrocœle the inclusion is not real but apparent, resulting from apposition of the open ends of two nervous half rings as in the case of the hydrocœle half rings just mentioned.

Anterior Cœlomic Regions.—In the stages immediately succeeding fixation, as the preoral lobe is rapidly shortened and the œsophagus ruptured, we find that the anterior cœlomic regions give rise to a relatively large cavity surrounding the œsophageal cone, entering the stalk and passing backwards into the right and left middle cœlomic regions (cf. Pl. 7, figs. 14, 17). Later, when the stalk lengthens, the contained cavity, as in normal development, keeps retreating towards the disc, so that except for a short funnel passing into its commencement, the stalk is now solid. We have to note that the main cavity just referred to, i. e. that derived from the anterior cœlomic regions, is a single space, not divided into right and left chambers. Later this cavity undergoes reduction and disappears after remaining for a time in widely open communication with the two **internal oral circular sinuses.**

Middle Cœlomic Regions.—Under this heading we have to notice hydropore, axial sinus, stone canal, axial organ, hydrocœle lobes, openings between posterior and middle cœloms, and internal oral circular sinuses (inner perihæmal rings). The **hydropore** is single and to the left in all my specimens, whether early and late, of double hydrocœle. The **axial sinuses** are symmetrical on the right and left sides except for the fact that the right sinus is not provided with a hydroporic canal. The tissue between the two sinuses becomes reduced at metamorphosis till it forms merely a thin septum between them. However, the sinuses in question do not communicate with each other at the end of metamorphosis, and accordingly we may be certain (as in the case of the hydrocœle ring canals and the internal oral circular sinuses) that they are derivatives of the middle cœlomic regions (cf. Pl. 7, fig. 16). We are justified in inferring that this also holds good in normal development on the left side for the structures named—a conclusion I had already reached (4, p. 276). The **stone canals** begin as grooves on either side, which become closed to form tubes opening at the ends into their respective hydrocœle half-ring canals and axial sinuses. It is noteworthy that on the right side the opening last referred to is still present, even though there is no pore canal related to it. The two stone canal grooves are illustrated in Pl. 7, figs. 10, 13, 16. The **axial organ** is present on the right as well as the left side and arises as in normal development, in the form of a loosely cellular fold of the wall of the middle cœlomic region parallel to the stone canal. The two folds unite aborally to form a single upper portion and head process. The latter is derived as normally from the spongy tissue underneath the dorsal sac, which becomes invaginated into the sac at metamorphosis and it corresponds, as I believe, to the heart of Balanoglossus. At the end of metamorphosis the two axial organs lie almost back to back against each other on either side of the septum mentioned above, as separating the two axial sinuses.

The ring canals of the **hydrocœle** becomes separated from the right and left middle cœlomic regions as occurs in normal development on the left side. The hydrocœle pouches expand rapidly at metamorphosis, becoming trilobed and then five-lobed as in normal development, at the time when the preoral region of the larva is undergoing retraction. The trilobed and five-lobed conditions represent stages respectively at which the rudiments of the terminal tentacle and of the first, or of the first and second, pairs of sucker feet are present. By the time a third pair of podial rudiments has appeared, the earliest formed pair is showing movements and beginning to serve for attachment. Ray I of the hydrocœle does not have the opportunity of associating itself with an aboral arm-rudiment, since, as was stated above, only four arm-rudiments are formed, namely, those which belong to rays II to V. The two hydrocœle rays I accordingly are found close together at the front end of the larva partly under the shelter of arm-rudiments II. A point of very great interest to be noted is that the ring canals of the two hydrocœles simply formed half rings, the extremities of which were close to, but not united with each other.

At the end of metamorphosis the right and left **internal oral circular sinuses** (inner perihæmal rings), like the two half-ring canals of the hydrocœle formed separate cavities. This goes to show that the sinuses in question are derived normally from the middle cœlomic regions alone, since, if the common anterior cœlomic region had shared in their formation, they ought not to have become separated from one another in double hydrocœle.

Right and Left Posterior Cœloms.—At metamorphosis the right and left posterior cœloms communicate with each other around the rectum and terminal part of intestine of the larva, as also dorsally across the middle line in front where their two anterior horns are in communication by a smaller or larger opening. During the course of metamorphosis these openings are not closed off, and accordingly the two hypogastric cœloms at the end of metamorphosis may be described as forming a single cavity all round. In cases where the disc is broad, the two layers of the longitudinal mesentery between the right and left posterior cœloms become widely separated, and the space left between them takes on a pseudo-cœlomic character, in the manner noted on p. 57. Accordingly what may be called a pseudo-epigastric cœlom (cf. Pl. 7, fig. 18), is produced underneath the middle area of the disc.

Pharyngeal Cœloms.—The origin of the two pharyngeal cœloms has already been referred to. They extend in the same manner as in normal development, and the mesentery between them and the posterior cœloms afterwards undergoes radial and interradial perforations, the strands which remain forming right and left sets of oral gastric ligaments. It was noted earlier that the two pharyngeal cœloms communicate with one another. This communication is on the anterior side of the œsophageal cone. At the end of metamorphosis the posterior extremities of the pharyngeal cœloms appear also to establish a communication between each other behind the point where the mouth develops, and thus in the end we have the pharyngeal as well as the hypogastric cœloms forming a circular cavity.

Perihæmal Pouches.—It was ascertained that the perihæmal pouches for interradii I–II arise from the posterior cœloms, as also do the pouches for II–III, III–IV, and

IV–V. The material available did not include stages giving conclusive evidence as regards I–V. Normally, in A. rubens, I had come to the conclusion (**4**, p. 260), that the perihæmal pouch I–II arises from the *l. p. c.* as in Solaster (**3**, p. 35), but the point was difficult to settle, owing to the proximity to the pouch of the opening from the *l. p. c.* into the *l. m. c.* In Asterina MacBride (**6**, p. 360), and Goto (**5**), and in Cribrella Masterman (**11**, p. 392), described the perihæmal pouch I–II as arising from the anterior cœlom. It is probable that the difference is connected with the presence of the communication above referred to, and that primitively all the perihæmal pouches belonged to the *l. p. c.*

Alimentary Canal.—It was established that in double hydrocœle, as in normal development, the **œsophagus** becomes divided near its junction with the buccal cavity and forms a cone projecting into the common expanded anterior cœlomic cavity (cf. Pl. 7, fig. 17). This cone is gradually incorporated with the stomach, and the new **mouth** forms in the neighbourhood of the former apex of the cone. As in normal development, the cardiac orifice of the stomach becomes gradually dilated. The anus and terminal part of the rectum degenerate leaving the intestine and first part of the rectum, the former being enclosed between the layers of the dorsal mesentery, and the latter projecting into the hypogastric cœlom posteriorly at the junction of the right and left components of this latter cavity. My material did not show the formation of a new anus, but there can be no doubt that, if formed, it would appear in the mid-ventral line behind the mouth outside the hydrocœle ring and under cover of the posterior edge of the "disc," i.e. the part formed by arm-rudiments V. The **pyloric sac** region became elongated at metamorphosis following the shape of the disc, and sent out right and left sets of pyloric cæca into the right and left arm rudiments. Four pairs of pyloric cæca were recognisable on each side, namely, those belonging to arm rudiments II–V. What became of the cæcal rudiments for ray I could not be made out with certainty. Probably they united together forming a single median anterior cavity seen, for example, in Pl. 7, fig. 18.

Unsymmetrical Double Hydrocœle. (Pl. 7, figs. 9, 18.)

Several examples of this condition were observed in early and late larvæ, as also after the completion of metamorphosis (Pl. 7, fig. 9). In every instance the right hydrocœle was smaller than the left one. In certain cases the full set of hydrocœle pouches was not present on the right side, the number being reduced to four or three or even to two. When only two were present they were usually, but not always, pouches III and IV. In every instance the right middle cœlomic region was not so large and did not hang so far back as in symmetrical double hydrocœle. As a consequence the left posterior cœlom expanded to a greater size than the right one, and accordingly, when the structures of the disc (aboral arm-rudiments and skeletal plates) began to be formed, these structures were not in the mid-dorsal line but were pushed to the right so as to encroach on the right side of the larval body. During the course of metamorphosis the inequality became more marked, and in extreme cases (cf. Pl. 7, fig. 9) the result was an almost apparently normal starfish-disc, which was made up of the five rays belonging to the left component, but was notched more or less deeply between arm-growths I and IV, and had the remains of the rays belonging to the right hydrocœle crowded together in the notch, especially towards the oral aspect. Comparison of several such instances leads to the conclusion that in normal development the last remains of a right hydrocœlic element, if such an element persisted, would have to be looked for on the oral side of the disc in interradius V–I, superficial to the hydrocœlic and perihæmal rings.

The specimen of unequal double hydrocœle shown in Pl. 7, fig. 9, possessed rudiments of the full set of five right hydrocœle pouches. The mouth was somewhat elongated and the stomach and pyloric cavity were single. An anus had not appeared. There was a well-developed dorsal sac to the dextral side of the single hydroporic canal as viewed aborally. There were two stone canals, each opening into its own axial sinus and ring canal. The axial sinuses did not communicate with one another, nor did the hydrocœles, nor did the internal oral circular sinuses (inner perihæmal rings). However, the oral nerve ring formed a complete circle around the mouth.

Frequency; Other Instances.

In 1912 I obtained only four double hydrocœle larvæ in all, but in 1913 the total number amounted to over sixty. Examples occurred in practically all my cultures, but were particularly numerous in two vessels, the larvæ in which happened to grow with great rapidity and to reach an unusual size. These larvæ were fed with Nitschia having a chance bacterial and flagellate infection. Six or seven of the larvæ went on to metamorphosis. Of ordinary plankton larvæ I have had the opportunity of examining a considerable number from the Firth of Clyde; several hundreds from St. Andrews Bay, through the kindness of Prof. W. C. McIntosh; and nearly a hundred sent me from the Little Belt by Dr. Th. Mortensen. Among all these not a single specimen of double hydrocœle was observed.

There seem to be no records of double hydrocœle from the **Crinoids** or **Holothurians.** Joh. Müller (1846, Taf. I, fig. 2d) referred to by Metschnikoff (**13**, p. 16) and MacBride (**7**, p. 578) figured an Ophiopluteus (obtained from plankton) which had a right as well as a left water vascular rosette, and to which he gave the name Pluteus paradoxus. In Amphiura squamata, the eggs of which develop within the parent, Metschnikoff (**13**) described the formation normally of a right as well as of a left hydrocœlic rudiment, and stated that the former sometimes went on to further differentiation. MacBride obtained examples of double hydrocœle larvæ in his cultures of Ophiothrix fragilis, and one such larva from plankton (7, p. 578, fig. 53).

As regards the **Echinoidea**, Metschnikoff (**14**, p. 64) mentions that he obtained from plankton near Messina a Spatangoid larva with two perfectly equal urchin plates, each having ambulacral feet and spines. In Echinus MacBride (**8**) has figured and described two very interesting double hydrocœle plutei. The first (E. miliaris) was about six weeks old and had an early "echinus-rudiment" and amnion cavity on the right side precisely similar to those on the left side, the arms and other structures of the larva being perfectly normal. The second specimen (E. esculentus) was about fifty-five days old and had right and left echinus-rudiments, the former being rather smaller than the latter. Both rudiments were sufficiently advanced to show the oral discs with the unpaired and paired tube feet, the nerve ring, groups of interradial spines, and the five dental pockets, with the mouth and œsophagus between them. As MacBride pointed out, in this case a practically complete set of definitely echinid structures were induced to form in the layers of the right side of the larva through the influence of an underlying right hydrocœle.

As regards **Asterids** we have to note that in 1874 Metschnikoff (**13**, p. 75) figured and described a late larva (referred by him to Asteracanthion, i. e., Asterias, but probably rather resembling the Astropecten type), which was provided with perfectly symmetrical right and left hydropores and hydrocœles. He made the very interesting suggestion that such larvæ showed a kind of symmetry which might well be compared with that of Ctenophores (see p. 74). MacBride in 1896 (**6**) described several examples of the double hydrocœle condition in Asterina, a starfish which has yolky eggs and direct development. No further examples in any starfish seem to have been recorded until 1912, when several appeared in my cultures of Asterias rubens (L.), and 1913, when they occurred in much greater numbers. Several advanced double hydrocœle larvæ were also obtained by me in 1913 from cultures of Porania pulvillus (O.F.M.), a species which, like A. rubens, has a feeding larva of the brachiolarian type.

Double Hydropore and Double Hydrocœle.

Double hydropore is not infrequently found in very early A. rubens larvæ, but, except in the rarest instances, the right hydropore disappears long before the stage at which double hydrocœle becomes evident. As a matter of fact, it would seem that double hydropore has little or nothing to do with the production of double hydrocœle in Asterias, since out of a total of over sixty double hydrocœle larvæ which I was able to pass under review, not a single one possessed two hydropores.[1] If, as seems entirely probable (**4**, p. 278), the hydrocœlic region of an Echinoderm corresponds to the left collar cavity of Balanoglossus, and the hydroporic canal to the proboscis pore, we may perhaps see in the independence of double hydropore and double hydrocœle an indication of the primitive independence of the anterior and the middle primary cœloms.

The frequency of double hydropore varies within the widest limits among different starfish, as among other Echinoderms (see **4**, p. 230). Thus in A. rubens the proportion in early larvæ is about one to ten as a maximum, but usually very much less. In A. glacialis, on the other hand, as also in A. vulgaris (Field, **2**, p. 111), most of the early larvæ in some cultures may develop two hydropores. The same thing is true in the case of Porania pulvillus. Among the Echinoids the larvæ of the regular urchins have only a single hydropore, while those of the common heart-urchin Echinocardium cordatum (MacBride, **9**) are very frequently, if not normally, provided with two. We cannot, therefore, ascribe the incidence of double hydropore directly to ancestral causes, but must set down its variations to the influence of **Homœosis** (see below under Causation).

[1] Two hydropores are, however, seen in the double hydrocœle larvæ figured by Metschnikoff (**13**, p. 74) and MacBride (**6**, p. 369).

Causation.

This is uncertain ground, and the following conclusions are simply put forward as appearing probable in the light of the evidence at present available.

My cultures (which were obtained from artificial fertilisations and reared by feeding with Nitschia) (**4**, p. 224) showed far greater numbers of double hydrocœle larvæ than occur in nature (p. 67). It is clear that something must have been at work to produce (*a*) disturbance of the normal course of development, and (*b*) deviation towards double hydrocœle. Under (*a*), as possible disturbing factors, we may single out (1) hurried nuclear maturation and probably also cytoplasmic immaturity in the ova employed, these having been shredded out from the ovary into sea water, where they underwent the nuclear maturation changes, and (2) defective or excessive nutrition of the larvæ. These factors could not, however, supply guidance in the production of double hydrocœle, and accordingly they are not truly causal of this condition, but only of developmental instability. However, we note further the following considerations coming under (*b*) above and making it seem natural for some at least of a group of unstably developing starfish ova to deviate into double hydrocœle:

(1) In the bilateral ancestor of Echinoderms the middle cœloms (from the left one of which the hydrocœle was derived) were no doubt symmetrical. The tendency to double hydrocœle may, therefore, have a directly atavistic foundation. It is not unreasonable to suppose that tendencies or potencies of ancestral origin may be strongly marked in ova that have undergone premature nuclear or cytoplasmic ripening.

(2) Distinguishable from directly atavistic potencies is the homœotic tendency to bilateral symmetry in the development of organisms, or of structures, which are normally no longer bilaterally symmetrical. There is evidence that this homœotic tendency may react so profoundly as to impose a particular

symmetry on the development of a species, although the symmetry in question is typically absent from the development of the group to which the species belongs. Certain facts in the incidence of double hydropore can best be explained on these lines; for example, the fact that in larvæ of the heart-urchin double hydropore is frequently, if not normally, found (MacBride, **9**), while larvæ of the common sea-urchin almost always show a single hydropore. We may use the term "primary homœosis" to indicate the tendency which produces the kind of symmetry manifested as regards the hydropore by the larvæ of Echinocardium.

(2) There is a somewhat different homœosis which may best be described as "secondary" or "casual," though it is probably of chief importance as a factor in the production of double hydrocœle. This kind of homœosis manifests itself later in development, getting the opportunity to do so through failure of a particular difference between the right and left sides to become established at the proper time, development thereafter proceeding on the same lines on both sides. The initial failure may be due to environmental causes, which in the case of double hydrocœle seem to be connected with nutrition (p. 54).

Conclusions.

(1) Homologies.—The structural details in double hydrocœle show that the dorsal sac is a mesial organ, always present in cases of double hydrocœle, and in no way corresponding with a right hydrocœle. Interradial ossicle I–II is also essentially a mesial structure and not in full morphological series with the remaining interradials. The larval right posterior (epigastric) cœlom is the equivalent of the larval left posterior (hypogastric) cœlom. The presence of two stone canals, pharyngeal cœloms and axial organ rudiments, and their relation to each other and to the dorsal sac afford confirmation of the view that the homology between Balanoglossus and Echinoderms extends to many details

of structure. According to this view, the dorsal sac is the equivalent of the pericardium in Balanoglossus, while the axial organ and pharyngeal cœlom are equivalent respectively to the left pharyngeal efferent vessel and the left pharyngeal cœlom of Balanoglossus (**4**, p. 278). Direct observation of the contractions of the floor of the dorsal sac in a double hydrocœle larva of Porania showed that they progressed from behind forwards.

(2) Light on Normal Development.—Confirmatory evidence has been obtained from the study of double hydrocœle regarding certain points that were somewhat difficult to make out in normal development. These points had reference to (1) the retention of the larval œsophagus (p. 66; **4**, p. 262); (2) the retention of the larval intestine and part of the rectum (p. 65; **4**, p. 263); (3) the formation of the hydrocœle and axial sinus and of the internal oral circular sinus entirely from the cœlom of the left side (*l. m. c.* as defined on p. 52); (4) the formation of perihæmal pouch I–II from the left posterior cœlom (p. 64; **4**, p. 260); (5) the view that hydrocœle pouch I should be looked upon as the most anterior and V as the most posterior of the hydrocœle lobes (p. 61; **4**, p. 276).

(3) Causation.—We may infer that (1) the ova employed were developmentally unstable from the cause stated (p. 70); (2) at a certain stage the *r. m. c.* was left isolated posteriorly like the *l. m. c.*, from a cause proximately connected with nutrition (p. 55); (3) thereafter the *r. m. c.* followed the same course of development as the *l. m. c.*, through secondary homœosis; (4) the great majority of double hydrocœles are to be accounted for in this manner, but we cannot exclude the possibility that, given initial instability, the influence of atavism and primary homœosis may sometimes be sufficiently strong to induce the formation of double hydrocœle apart from the action of environmental factors.

(4) The Bilateral Ancestor of Echinoderms.—The probable characters of the ancestor are discussed elsewhere in connection with normal development (**4**, p. 279). The

double hydrocœle series described in the present paper shows us, in the most primitive type of Echinoderm larva, bilaterality carried much further than it is normally in this or any other larval type within the phylum. The data from double hydrocœle accord with the view that there has been a fixed stage in the evolution of Echinoderms; that fixation took place in the middle line of the preoral lobe; and that, as in Antedon, freedom was obtained by loss of the attaching stalk. On the other hand, the Pentactæa theory of Semon (**16**) receives no kind of support. Although not all the structures which are found in double hydrocœle after metamorphosis can be put down as proto-echinodermal in phylogeny, still I would include among such structures the dorsal sac, the two axial organ rudiments, and the two pharyngeal cœloms. Probably the two sets of pyloric cæca and the dorsally-convex protecting shield with its calcareous plates (cf. Pl. 6, fig. 5) should also be included. It will be remembered that in Antedon the stomach is provided with out-pocketings which may be compared with the radial cæca. Information regarding double hydrocœle in crinoid larvæ, especially if metamorphosis supervened, would be of extreme interest. The fact that even now a double hydrocœle starfish larva can undergo complete metamorphosis and remain capable of life favours the possibility that free bilaterally symmetrical Proto-echinoderms with right and left sets of food-collecting grooves, and with the other structures just referred to, may have appeared in early geological times.

Some such form, perhaps at first creeping but afterwards becoming attached by the preoral lobe, might well prove a starting-point for the differentiation of the primitive Crinoids from the primitive Asteroids. Certain obvious objections, based on habit, against deriving starfish as we know them from the stock in question will be greatly lessened, if not removed altogether, should the first results of feeding experiments at present in progress be ultimately fully confirmed. These results show that certain starfish, e. g. Porania, are able to collect and ingest food particles by means of their actinal ciliation, healthy survival for considerable periods of time without loss of weight being thereby permitted. Observation of the ciliary currents, etc., in these starfish show that the currents in question actually bring particles to the mouth.

The sharp *ventral* curvature of the alimentary canal in the late brachiolaria and at the end of metamorphosis in double hydrocœle, no doubt marks a contrast, which, appearing early between the primitive Echinoderms and the Enteropneusts and Pterobranchs, became extreme as regards the last-named stock when the equally sharp *dorsal* curvature of the gut in this stock was established.

The immediate ancestor of the phyla named was, of course, a truly cœlomate animal, with primitive metameric segmentation and with separate mouth and anus. Probably, also, the different cœlomic cavities arose independently from the archenteron (**4**, p. 234). If we try to go still further back, we can only follow the well-known view which assumes that the cœloms are gastrovascular spaces that have become separated off from the digestive cavity, and that the gastrula opening has given rise by constriction to the mouth and anus. Masterman (**10**) derived the primitive metameric (or archicœlomatous, to use his own term) type directly from a tetramerous cœlenterate symmetry, and showed schematically how the arrangement of the cœloms in the higher phyla could thus be accounted for. On the other hand, Metschnikoff (**13**, p. 73) in 1874 called attention to the remarkable parallel that can be drawn between a double hydrocœle Asterid larva with two hydropores and such a Ctenophore as Cydippe; the hydropores, hydrocœle rays, and posterior cœloms of the former finding equivalents in the excretory pores, meridional canals, and paragastric tubes of the latter, while, in both, the digestive and cœlomic cavities take origin from similarly placed regions of the archenteron. MacBride has lately (**7**, p. 593), in the light of recent work on the relationships of Ctenophores, laid further emphasis on the possible Ctenophore affinities of the early ancestor of the Cœlomata.

References.

1. Bateson, W.—'Materials for the Study of Variation,' London, MacMillan, 1894.
2. Field, G. W.—"The Larva of Asterias vulgaris," London, 'Quart. Journ. Micr. Sci.,' 34, 1892, pp. 105-128.

3. Gemmill, J. F.—"The Development of the Starfish Solaster endeca Forbes," London, 'Trans. Zool. Soc.,' pt. i, 1912, pp. 1–71.

4. ——— "The Development of the Starfish Asterias rubens, L.," London, 'Trans. Roy. Phil. Soc.,' 1914, pp. 213–294.

5. Goto, S.—"Some Points in the Metamorphosis of Asterina gibbosa," Tokyo, 'Journ. Coll. Sci.,' xii, pt. iii, pp. 227 et seq.

6. MacBride, E. W.—"The Development of Asterina gibbosa," London, 'Quart. Journ. Micr. Sci.,' 38, 1896, pp. 339–411.

7. ——— "The Development of Ophiothrix fragilis," London, 'Quart. Journ. Micr. Sci.,' 51, 1907, pp. 557–606.

8. ——— "Two Abnormal Plutei of Echinus," London, 'Quart. Journ. Micr. Sci.,' 57, pp. 235–250.

9. ——— "Studies in the Development of the Echinoidea II. The Early Larva of Echinocardium cordatum, and the result of crossing the Species with Echinus esculentus," London, 'Quart. Journ. Micr. Sci.,' 58, pp. 299–324.

10. Masterman, A. T.—"On the Theory of Archimeric Segmentation and its bearing upon the Phyletic Classification of the Cœlomata," Edinburgh, 'Proc. Roy. Soc.,' xxii, 1898, pp. 270–310.

11. ——— "The Early Development of Cribrella oculata Forbes, with Remarks on Echinoderm Development," Edinburgh, 'Trans. Roy. Soc.,' xl, 1902, pp. 373–417.

12. Metschnikoff, E.—"Studien über die Entwickelung der Echinodermen u. Nemertinen," St. Petersburg, 'Mem. Ac. Sci.,' xiv, Ser. 7, No. 8, 1869, pp. 1–73.

13. ——— "Studien über die Entwicklung der Medusen und Siphonophoren," 'Zeitschr. Wiss. Zool.,' xxiv, 1874, pp. 1–83.

14. ——— "Embryologische Mittheilungen über Echinodermen. III. Zur Kenntniss der Wassergefässanlage bei Asteriden u. Echinoiden," 'Zool. Anz.,' vii, 1884, pp. 62–65.

15. Müller, Joh.—"Ueber die Larven u. die Metamorphose der Echinodermen, etc.," Berlin, 'Abh. Ak. Wiss.,' 1846, Taf. i, fig. 2 *d*.

16. Semon, R.—"Die Entwickelung der Synapta digitata und die Stammesgeschichte der Echinodermen," 'Jen. Zeitsch, Natw.,' xxii, 1885, pp. 175–302.

EXPLANATION OF PLATES 6 AND 7,

Illustrating Mr. James F. Gemmill's paper on "Double Hydrocœle in the Development and Metamorphosis of the Larva of Asterias rubens, L.

Lettering and Abbreviations employed.

1, 2, 3, 4, 5, 6.—The larval cillated processes in order as follows: 1. Median dorsal: 2. anterior dorsal; 3. posterior dorsal; 4. postero-lateral; 5. post-oral; 6. preoral.

I, II, III, IV, V.—Lead by continuous lines to hydrocœle pouches I, II, etc., and by dotted lines to arm-rudiments I, II, etc.; (*r*) and (*l*) after these numerals indicate respectively that the structures referred to belong to the right or to the left side.

a. c. Common united portion of the right and left anterior cœloms. *ant. br.* Anterior brachium. *anus.* Anus. *ax. org.* Axial organ. *ax. s.* (*l.*) Left axial sinus. *ax. s.* (*r.*) Right axial sinus. *b.* I–II. Basal or interradial ossicle I–II. *b.* II–III, etc., (*r*) or (*l*) Right or left interradial ossicle II–III, etc. *b. c.* Buccal cavity. *br.* The three brachia. *d. arm. r.* Aboral or disc arm-rudiments. *d. c.* Opening between dorsal horn of posterior cœlom and left middle cœlom. *d. h. l. p. c.* Dorsal horn of left posterior cœlom. *d. h. p. c.* In fig. 3 is over place of fusion of dorsal horns of right and left posterior cœloms. *hy.* Cavity belonging to hydrocœle. *hy.* I, II, III, etc. (*r.*) or (*l.*) Right or left hydrocœle pouches, I, II, III, etc. *hy. can.* Hydroporic canal. *hy. circ.* Circular canal of hydrocœle. *hyp. c.* Hypogastric cœlom. *int.* Intestine. *int. or s.* Internal oral circular sinus (inner perihæmal ring). *l. a. c.* Left anterior cœlom. *lat. br.* Lateral brachium. *l. hy.* I, II, III, etc. Radial pouches I, II, III, etc., of the left hydrocœle. *l. m. c.*, or *l. m. c.* (*l. hy.*) Left middle cœlomic region. *l. p. c.* Left posterior cœlom. *m.* Mouth. *n. r.* Nerve ring. *œs.* Œsophagus. *pap.* Papillæ beside sucker. *perih.* Perihæmal pouches of outer perihæmal ring. *phar. c.* and *phar. c.* (*l*) or (*r*) Pharyngeal cœlom and left or right pharyngeal cœlom. *po. cil. bd.* Post-oral ciliated band. *pod. l. hy.* or *pod. r. hy.* Sucker feet of the left or right hydrocœle. *pr. cil. bd.* Preoral ciliated band. *pr. l.* Preoral lobe. *ps. epg. c.* Pseudo-epigastric cœlom (see p. 64). *pyl. s.* Pyloric sac. *r. a. c.* Right anterior cœlom. *rect.* Rectum. *r. hy.* Right hydrocœle. *r. hy.* I, II, etc., Radial pouches I–II, etc., of right hydrocœle. *r. m. c.* or *r. m. c.* (*r. hy.*) Right middle cœlomic region or right hydrocœlic region. *r. p. c.* Right posterior cœlom. *s.* Sucker. *st. c.* (*l*) or (*r*) Left or right stone canal. *stk.*

Attaching stalk. *stom.* Stomach. *t.* II, III, etc. (*l*) or (*r*) Left or right terminal ossicle of rays II, III, etc. *ves.* Dorsal sac or madreporic vesicle. *v. h. l. p. c.* Ventral horn of the left posterior cœlom. *v. h. r. p. c.* Ventral horn of the right posterior cœlom. *w.* Small piece of sea-weed.

PLATE 6.

Fig. 1.—Ventral view of normal larva about thirty-five days old showing hydrocœle lobes on left side, isolation of the right posterior or epigastric cœlom, and union of ventral horn of *l. p. c.* with right middle cœlomic cavity. The general description of this stage is given on pp. 52, 53.

Fig. 2.—Ventral view of double hydrocœle larva in which the right and left set of hydrocœle pouches have appeared. The two posterior cœloms are completely separated from the middle cœlomic regions, and their ventral horns have met and united with one another across the mid-ventral line between stomach and rectum, and have also sent round folds to enclose the rectum. Posteriorly the thickening due to the double set of aboral arm-rudiments is only shown in optical section and not in surface view.

Fig. 3.—Double hydrocœle larva a little further advanced than in last fig., and from the dorsal aspect. It will be seen that the two posterior cœloms have united with one another in front across the mid-dorsal line, and that each has acquired a secondary opening into the corresponding hydrocœle. The dorsal sac is elongated, and lies almost exactly in the middle line. In this specimen all the ciliated processes on the right side are somewhat smaller than those on the left, a condition not infrequently found in A. rubens larvæ apart from double hydrocœle. As in fig. 2 the disc thickening is shown only in optical section.

Fig. 4.—View, from dorsal side, of late double hydrocœle brachiolaria in which the rudiment of the disc is particularly broad, and, instead of having only the terminal ossicles on each side, shows also the interradials. The latter are in pairs, except that a single one, overlying the dorsal sac, represents the two we might have expected for interradius I–II (see p. 57). The rest of the interradials appear in the epiderm over a pseudo-cœlomic space which lies between the two layers of the dorsal mesentery, and is of the same nature as that shown in fig. 18 (see p. 57 and p. 64). Each of the terminals carries the usual number of spines.

Fig. 5.—Lateral view of double hydrocœle larva at the very commencement of metamorphosis and before attachment has taken place.

The contractions of the body-wall, which produce swelling of the anterior cœlomic cavity and shortening of the preoral lobe, have just begun. On the preoral lobe an unusual arrangement of papillæ is present such as also occurs by way of variation in otherwise normal larvæ. The edges of the four arm-rudiments belonging to the left side are seen, each already showing the characteristic mesial notch.

Fig. 6.—View from ventral and slightly from left side, of double hydrocœle larva which attached itself temporarily and crawled for some distance with the help of the brachia and sucker in the manner described on p. 59. The disc rudiments are here relatively narrow, forming a contrast with those shown in fig. 4.

PLATE 7.

Fig. 7.—View from left side of double hydrocœle larva about twenty hours after metamorphosis has begun. The preoral lobe is now greatly retracted, and the ciliated processes are gradually disappearing, while the sucker is still somewhat prominent. It will be seen that the remains of the posterior ciliated band are within the circle of the hydrocœle lobes and apparently very much in the position where the oral nerve tract may be expected to form. However, examination of serial sections of different larvæ has made it practically certain that this band has nothing to do with the origin of the nerve-tract in question. As in fig. 5 the edge of the disc-rudiments is seen from the left side, only four rudiments being present, namely rudiments II–V. It will be understood that the larva would show the same appearance if viewed from the right side. Note at the anterior end the cavity of the dorsal sac and the shading to indicate the pore canal.

Fig. 8.—Young double hydrocœle starfish near end of metamorphosis as seen from left side. The slender stalk connecting the sucker with the body is seen, the insertion of the stalk being in the mid-ventral line and somewhat in front of the middle of the larva. Rupture of the stalk took place near its junction with the body as in normal development. The five hydrocœle rays belonging to the left side of this bilateral starfish are seen in the drawing, a corresponding set being present on the right side. The young starfish was more convex dorsally than is shown in the illustration (p. 62).

Fig. 9.—View from ventral aspect of an asymmetrical double hydrocœle starfish, after metamorphosis. The remains of the stalk have disappeared and the mouth is formed. The latter is somewhat curious in shape since it almost divided into two unequal parts by a fold or constriction which leaves the major opening in connection with the original left set of disc and ray structures. The smaller (right) set of rays occupies a wedge-shaped interval between pouches I and V and

arm-rudiments II and V of the larger (left) series. The vesicular appendage seen to the left of arm-rudiment V may represent a rudimentary arm-rudiment I in the original left series. Had it been fully developed and unhindered by the right hydrocœle, it would have travelled round in order to become associated with hydrocœle pouch I and thereby complete a normal starfish disc.

Fig. 10.—Transverse section through hydroporic region of the larva shown in fig. 7. Note in particular the single hydroporic canal and dorsal sac, the two stone canals and pharyngeal cœloms, and also the two extensions of the posterior cœloms which almost meet on the dorsal aspect of the rectum.

Fig. 11.—Transverse section of same larva but further forward, and showing opening of œsophagus into stomach, hydrocœle pouches I and V, the two pharyngeal cœloms and the single dorsal sac.

Fig. 12.—Transverse section of same larva but considerably further back, and passing through the dorsal opening between the *l. p. c.* and the *r. p. c.* The hydrocœle pouches are II (dorsally) and III (ventrally) on either side.

Figs. 13, 14, and 15.—Three transverse sections through the larva in early metamorphosis shown in fig. 6. In fig. 13 the section passes through the anterior portion of the junction between stalk and body, and cuts symmetrically the right and left posterior cœloms, hydrocœles, stone canals and pharyngeal cœloms. The mesial portion of the pharyngeal cœlom is seen. Fig. 14 passes a little behind the middle of the stalk and cuts the œsophagus along its full length as well as the dome of the buccal cavity. The latter still opens freely to the surface, further back than the level of the section. Fig. 15 is still further back in the series and passes through the anal opening, which is here seen in process of occlusion. For a short distance up from this opening, the wall of the rectum will also degenerate leaving, however, a portion of the rectum as well as the intestine of the larva to give rise to the rectal sac and intestine after metamorphosis.

Figs. 16 and 17.—Two transverse sections through a double hydrocœle larva in the middle stage of metamorphosis, to be compared respectively with figs. 13 and 14. Note in particular the fact that perihæmal pouch I–II on either side is arising from the posterior cœlom, and also that the rudiments of the two axial organs are appearing in front of their respective stone canals. In fig. 17 the œsophagus has become divided and the circular canal of the water vascular system is beginning to be constricted off from the *l. m. c.* Figs. 13–17 may, with advantage, be compared with figs. 27, 28, in my account of the normal development of Asterias rubens (**4**).

Fig. 18.—Vertical section through disc of the asymmetrical double

hydrocœle specimen described on p. 66, and illustrated in fig. 9. The section looks almost a normal one (cf. **4**. Pl. 24, Fig. 31), but the portions of hydrocœle seen on opposite sides belong to different systems, that on the right side of the figure (including axial organ, stone canal and axial sinus) being part of the smaller right hydrocœle complex, while on the opposite side we have the left hydrocœle, etc. Note on the aboral side of the stomach a large pseudo-epigastric cœlomic space (see pp. 57, 64).